RESEARCH ARTICLE

Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts?

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Abstract

Invasions by non-native species are a threat to biodiversity because invaders can impact native populations, communities and entire ecosystems. To manage this threat, it is necessary to have a strong mechanistic understanding of how non-native species affect local species and communities. We reviewed 259 published papers (1972–2012) that described field experiments quantifying the impact of aquatic non-native species, to examine whether various types of study biases are limiting this understanding. Our review revealed that invasion impacts had been experimentally quantified for 101 aquatic non-native species, in all major freshwater and marine habitats, on all continents except Antarctica and for most higher taxonomic groupings. Over one-quarter (26%) of studies included tests for impacts on local biodiversity. However, despite this extensive research effort, certain taxa, habitats and regions remain poorly studied. For example, of the over one hundred species examined in previous studies, only one was a marine fish and only six were herbivores. Furthermore, over half (53%) of the studies were from the USA and two-thirds (66%) were from experiments conducted in temperate latitudes. By contrast, only 3% of studies were from Africa and <2% from high latitudes. We also found that one-fifth (20%) of studies were conducted in estuaries, but only 1% from coral reefs. Finally, we note that the standard procedure of pooling or not reporting non-significant treatments and responses is likely to limit future synthetic advancement by biasing meta-analysis and severely limiting our ability to identify non-native species with none or negli-

gible ecological impacts. In conclusion, a future focus on poorly-studied taxa, habitats and regions, and enhanced reporting of results, should improve our understanding and management of impacts associated with aquatic non-native species.

Keywords
Biotic homogenization, alien species, exotic species, review

Introduction

Invasion by non-native species can alter community structure and ecosystem functions with significant impacts on biodiversity (Wilcove et al. 1998; Grosholz 2002; Olden et al. 2004; Bruno et al. 2005; Byers 2009) and large economic (Pimentel et al. 2000), and cultural costs (Lockwood et al. 2007). Efforts to manage and mitigate invasion impacts are contingent on rigorous scientific evidence for the underlying drivers of change (Underwood 1996; Byers et al. 2002; Sutherland et al. 2004). There is debate, however, about whether non-native species cause environmental change, respond to environmental change or do both with complex feedback interactions (Gurevitch and Padilla 2004; Didham et al. 2005; Simberloff 2011). Experimental approaches, where the identity and density of non-native species are controlled, can provide much-needed causal linkages between the non-native species and ecological changes in invaded ecosystems and habitats.

The discipline of invasion ecology has grown immensely in recent decades with papers published across an increasing number of general scientific (ecology, invasion biology, conservation biology) and subject-specific (terrestrial, freshwater and marine) journals. Recently, Pyšek et al. (2008) tallied >2500 papers published on the topic of invasion ecology. Furthermore, it appears that invasion impacts have been reviewed in greater detail for terrestrial than aquatic ecosystems; e.g., recent reviews of plant invasion impact did not include examples from marine seaweeds or seagrasses (cf. reviewed reference listings, Powell et al. 2011; Vilà et al. 2011; Pyšek et al. 2012). To be able to build strong and general impact models and theories across ecosystems it is important that aquatic impact studies are similarly evaluated. Indeed, there is growing scientific evidence that invasions by non-native species are prolific in aquatic ecosystems (Carlton 1996; Hewitt and Campbell 2010; Strayer 2010). Furthermore, even if new aquatic invasions are curbed, impacts from past invaders may continue to increase as lag-phases transition into exponential phases, and ecological interaction "debts" are "collected" over time (Sax and Gaines 2008; Kuussaari et al. 2009). Existing reviews of aquatic invasion impacts have focused so far on specific taxonomic groups (e.g., Ward and Ricciardi 2007; Thomsen et al. 2009; Cucherouset and Olden 2011; Twardochleb et al. 2013), regions (e.g., Ricciardi 2006; Ruiz et al. 2011) or tested specific ecological questions (e.g., Ricciardi and Atkinson 2004; Grosholz and Ruiz 2009; Thomsen et al. 2011). However, to date there has been no synthesis of invasion impacts across non-native taxa, regions and habitats in aquatic ecosystems, thereby limiting our capability to evaluate progress and target research gaps.

Our objectives were to quantify the breadth of field-based experimental studies on invasion impacts in aquatic ecosystems, to identify what species, regions and environments have been targeted in these tests, and whether there have been any general problems relating to their experimental design and data reporting. Analogue reviews have provided important knowledge about research biases in other fields, including climate change, terrestrial ecology, conservation biology and general invasion biology (Pyšek et al. 2008; Darwall et al. 2011; Martin et al. 2012; Wernberg et al. 2012; Kimbro et al. 2013; Sorte et al. 2013).

To achieve our objectives, we reviewed field-based experiments on invasion impacts to identify what species, regions and environments have been targeted in these tests, and whether there have been any general problems relating to their experimental design and data reporting. We hope that this review will stimulate experimental research about aquatic invasion impact and this will lead to the development of new predictive tools in conservation management.

Methods

We searched for peer-reviewed, manipulative aquatic field experiments in Web of Science, Current Contents, and Google Scholar, using various combinations of 'impact', 'effect', 'non-native', 'non-indigenous', 'exotic', 'invader', 'alien', 'aquatic', 'marine', and 'freshwater'. Reference lists were back-tracked from existing review papers and frequently cited impact studies (e.g. Bruno et al. 2005; Williams and Smith 2007; Byers 2009). We stopped searching on 1ˢᵗ of July 2012 to allow a definitive analysis, as new impact studies are being published every month. Field conditions were defined as any outdoor setting exposed to natural cycles of temperature and light (Martin et al. 2012). We included all studies that quantified impacts on resident organisms by comparing 'invaded treatments' to 'non-invaded controls' using addition or removal of the non-native species (Thomsen et al. 2011), including whole-lake experiments where non-native species (typically trouts) had been removed or added in well-documented events to specific lakes (treatments) but not to others (controls) (Pope et al. 2009). We also included studies published in non-invasion related contexts, for example impacts of "drift algae", "turf algae", or "grazers", if the manipulated organisms were entirely dominated by non-native species, such as *Gracilaria vermiculophylla*, *Wommersly setacea*, and *Littorina littorea*, respectively (Bertness et al. 1999; Airoldi 2000; Thomsen and McGlathery 2006).

First, we evaluated the published research in relation to the *attributes of individual studies*. We categorized whether the journal in which experiments were published targeted general scientists, freshwater, marine, or aquatic biologists (see Suppl. material 1 for detail). We recorded the year of publication and determined whether the experimental design was spatially pseudo-replicated (i.e. with only one 'spatially independent' control and/or treatment, Hurlbert 1984), and if the study reported an average invasion impact on resident organisms with an associated measure of

variation (e.g., SD, SE or CL). We specifically identified community impact studies because these are few in numbers but highly valued (Parker et al. 1999; Vilà et al. 2011). For each identified community study we counted if an impact was reported using multivariate structures from graphs (e.g. nMDS plots) or inferential tests (e.g. Anosim) and on univariate biodiversity metrics including taxonomic richness, diversity and evenness.

Second, we evaluated study characteristics related to the *attributes of the non-native species*, that is whether the non-native species was a plant or animal, pre-dominantly occupied the pelagic or benthic realm, was mobile or sessile, whether its trophic position was a plant, filter-feeder, herbivore, omnivore or carnivore, and its taxonomic affiliation. We classified very slow-moving bivalves as sessile taxa, and grouped consumers of macroscopic or microscopic primary producers (the latter group includes sediment eaters and detrivores) together to represent herbivores.

Third, we evaluated study characteristics related to the *attributes of the invaded system*. Here we extracted data about the spatial location of each experiment. Studies that included nested designs or multiple experiments, where study sites were separated by >1 km, were added as independent locations. These data were also grouped into invaded continent and latitude (proxy for climate). We then noted if the invaded system was a freshwater or marine habitat, where estuaries and salt marshes were grouped as marine. This attribute represents the invaded system (instead of the non-native species) because the same non-native species (e.g., the common reed *Phragmites australis*) can impact both marine and freshwater habitats. These two broad habitat types were subdivided into streams, ponds, lakes, wetlands, estuaries, open coast marine sands, rocky intertidal, or rocky subtidal, where wetlands included a few riparian studies, ponds included experiments conducted in outdoor freshwater mesocosms (ponds and mesocosm experiments are both conducted in relatively small enclosed systems), estuaries included both intertidal and subtidal studies, and the rocky subtidal zone included a few coral reef experiments (too few to justify a separate analysis for this habitat, see discussion for detail).

Finally, we examined if taxa were studied in proportion to their 'recognized occurrence as non-native species'. We used Hewitt and Campbell's (2010) tally of marine non-native species (this is a 'grey literature' report, but represent the most comprehensive tally to date), i.e. we tested if some taxa are well-recognized as non-native species but never studied. This comparison was only done for marine organisms because no master list exists for freshwater non-native species. We first regrouped invaded regions into geographical units used by Hewitt and Campbell (2010; 18 marine provinces based on biological similarity) and then conducted linear regression between our data to data listed in Hewitt and Campbell (2010, Fig. 2 and 11). We used Type 1 regression because our objective was to provide simple predictive models (Quinn and Keough 2002), and we forced the line through the origin because there can be no impact study if there is no invasion (the greater the slope, the more field experiments have been conducted relative to known marine non-native species).

Results

Our initial search suggested that more than 700 aquatic invasion impact studies have been published. However, after excluding reviews (Williams and Smith 2007; Thomsen et al. 2009), indoor lab experiments (Hoeffle et al. 2011), and correlative studies (Staehr et al. 2000; Forrest and Taylor 2003) 259 manipulative field-based impact experiments remained. These peer-reviewed papers experimentally quantified invasion impact on 101 aquatic non-native species and on 4 invasive taxa above the species level ('*Dreissena* mussels', 'trouts', 'predatory fish', and 'crabs', for brevity we also refer to these taxa as non-native 'species'). A total of 20 aquatic non-native species have been experimentally manipulated in more than 5 studies (Suppl. material 1), with 5 species being studied 10 times, including *Carcinus maenas* (a marine crab, 18 studies), 'trouts' (combined effects of freshwater *Oncorhynchus mykiss* and *Salvelinus fontinalis*, 12 studies), *Littorina littorea* (a marine snail, 11 studies), *Pacifastacus leniusculus* (a freshwater crayfish, 11 studies), and *Dreissena polymorpha* (a freshwater mussel, 10 studies).

Evaluating research in relation to *study attributes* revealed that many more papers were published in journals targeting general readers (130) than marine (61), freshwater (41) or freshwater and marine (27) readers. Publications of invasion impact papers increased rapidly for all journal types (Fig. 1a). The first study was published in 1972 (Hurlbert et al.), but very few studies were published in the 1970s (total of 2 species; 3 studies) or 1980s (8; 11). However, experimental approaches to testing invasion impacts became common in the 1990s (28; 43) and increased dramatically in the 2000s (79; 158). From 2010–2012 we identified experiments on 35 species in 44 studies. This trend corresponds to a general exponential decadal increase in published aquatic field-based invasion impact studies (r^2 = 0.99, p = 0.0006). Of the 259 impact papers, 12 were spatially pseudo-replicated or did not replicate treatment and/or control plots (Fig. 1b) and 22 did not report any variability around reported average impacts (Fig. 1b). We found 68 studies that reported impacts on multivariate or univariate community metrics (Fig. 1c), of which 35 quantified impact with multivariate plots, 32 with multivariate inferential tests, 52 on richness, 23 on diversity and 10 on evenness. Only two of the 68 studies reported all 5 community metrics (Hejda and Pyšek 2006; Albins 2013).

Furthermore, when we evaluated study characteristics in relation to *invader attributes* we found that more experiments have been done on non-native animals (75 species, 185 studies) than plants (30, 76) (Fig. 2a), on benthic (83, 199) than pelagic (22, 64) invaders (Fig. 2b), and on almost the same number of sessile (54, 116) and mobile (51, 143) invaders (Fig. 2c). Subdividing non-native animals into trophic position showed that carnivores (25, 73) were more studied than filter-feeders (27, 46) and omnivores (14, 44), and that few invasive herbivores and detrivores have been studied (10, 29) (Fig. 2d). Of these 10 species, 6 were herbivores with a capacity to denude large vegetation (the mammal *Myocastor coypus*, the bird *Cygnos olor* and the four snails *Littorina littorea*, *Bellamya chinensis*, *Physella acuta*, *Pomacea canaliculata*), whereas the
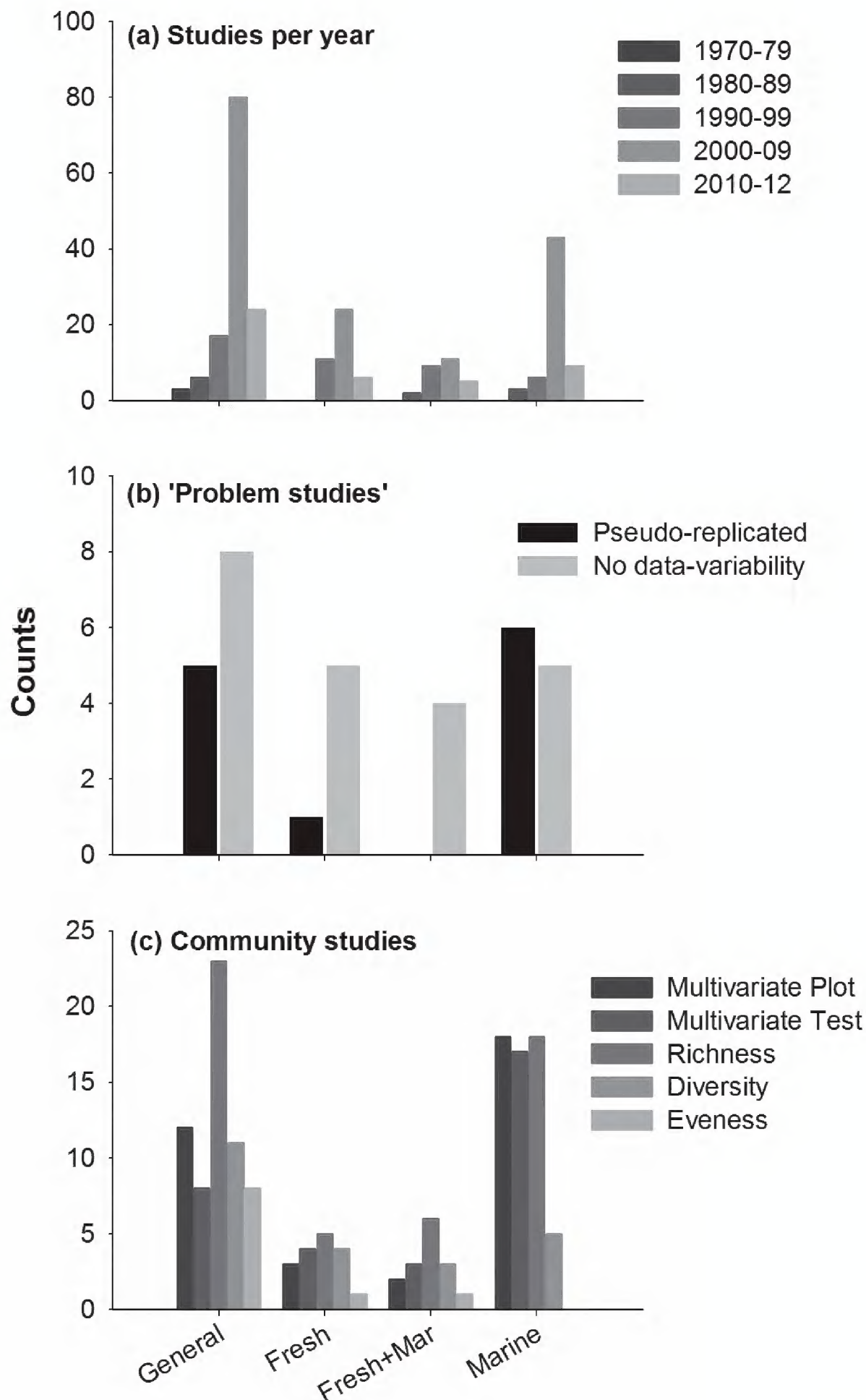
Figure 1. Aquatic invasion impact experiments published in general, freshwater, marine, and both freshwater and marine journals (see S1 for journal classification) **a** decadal trend in publication rates (the last bar only include studies published 2010–12) **b** Studies where the experimental design was spatially pseudo-replicated or did not replicate treatment or control plots, and studies that did not report any measure of variability for impact data **c** Community impact studies that quantified impact with graphical display, multivariate inferential tests, or on taxonomic richness, diversity or evenness.

remaining 4 non-native species were sediment-eaters and detrivorous snails and crustaceans (*Batillaria attramentaria*, *Ilyanassa obsoleta*, *Potamopyrgus antipodarum*, *Limnomysis benedeni*). The most frequent experiments were on non-native fish (20 species, 58 studies - where two studies were from marine systems and the lionfish *Pterois volitans*), vascular plants (20, 38) molluscs (18, 55), crustaceans (16, 53) and algae (10, 39). By contrast, relatively few experiments were on non-native tunicates (8 species, 7 studies), annelids (3, 7), amphibians (3, 5), mammals and birds (3, 5), bryozoans (2, 3), echinoderms (1, 3) or reptiles (1, 3) (Fig. 2e).

Evaluating study characteristics in relation to the *invaded system attributes* showed a strong geographical pattern (Fig. 3); impacts documented in the 259 papers represent studies from 30 countries and were strongly dominated by the USA (60 species; 137 studies). Furthermore, only 9 other countries have tested for impacts of ≥5 non-native species, including Australia (13; 21), Germany (8; 7), Brazil (6; 4), Canada (8; 11), Japan (6; 5), New Zealand (6, 5), Italy (5; 12), Spain (5; 10), and France (5; 4). This geographical pattern was also evident when grouped into continental scales; invasion impacts have been tested mainly in North America (59 species, 145 studies), Europe (30; 54), and Australasia (19; 26). Far fewer non-native species have been tested from South America (13; 10), Asia (8; 11), Africa (4; 8) and various islands (4; 5) (Fig. 3, 4a).

We also found a strong geographical pattern along a latitudinal (climate-related) gradient; most studies were from the mid-latitudes of 35–46° (69 species, 171 studies), followed by 23–34° (24; 36) and 47–58° (21; 33). By contrast, few non-native species have been studied from tropical or cold/polar regions (0–22° = 12 species, 14 studies; 59–90° = 5 species, 5 studies – and these studies were all from 59–64° N) (Fig. 3, 4b). Finally, we found that more studies have been conducted in freshwater (59 species, 143 studies) than marine (48; 116) habitats (Fig. 4c), or more specifically, that most aquatic invasive species have been studied in ponds (33; 43, including mesocosm experiments), followed by estuaries (30; 53), streams (18; 43), wetlands (15; 24), rocky subtidal (16; 21, including 3 species and 4 studies from coral reefs), lakes (15; 33), rocky intertidal (12; 32), and sandy open subtidal habitats (7; 11) (Fig. 4d).

Finally, when we compared our data to Hewitt & Campbell's compilation of marine non-native and cryptogenic species we found a significant slope, indicating that the number of marine species grouped into different invasive taxa (Fig. 5c; slope = 0.022, p = 0.0001, n = 17) and invaded biogeographical regions (Fig. 5d; slope = 0.021, p = 0.0006, n = 18) correlated with number of taxa and regions tested in manipulative field experiments. However, even though the line fit well generally, there were still over and under-represented taxa; for example, experimental studies on molluscs, angiosperms and chordates (mainly tunicates) were over-represented (well above the line), whereas fish, crustaceans and cnidarians were under-represented (well below the line). Similarly, experimental studies from the North East Pacific and the North West Atlantic were over-represented, whereas experimental studies from the Southern Pacific Ocean and the Mediterranean Sea were under-represented. Both regression slopes were small, showing that ca. 2 non-native species had been tested in field impact-experiments for every 100 known non-native marine species.
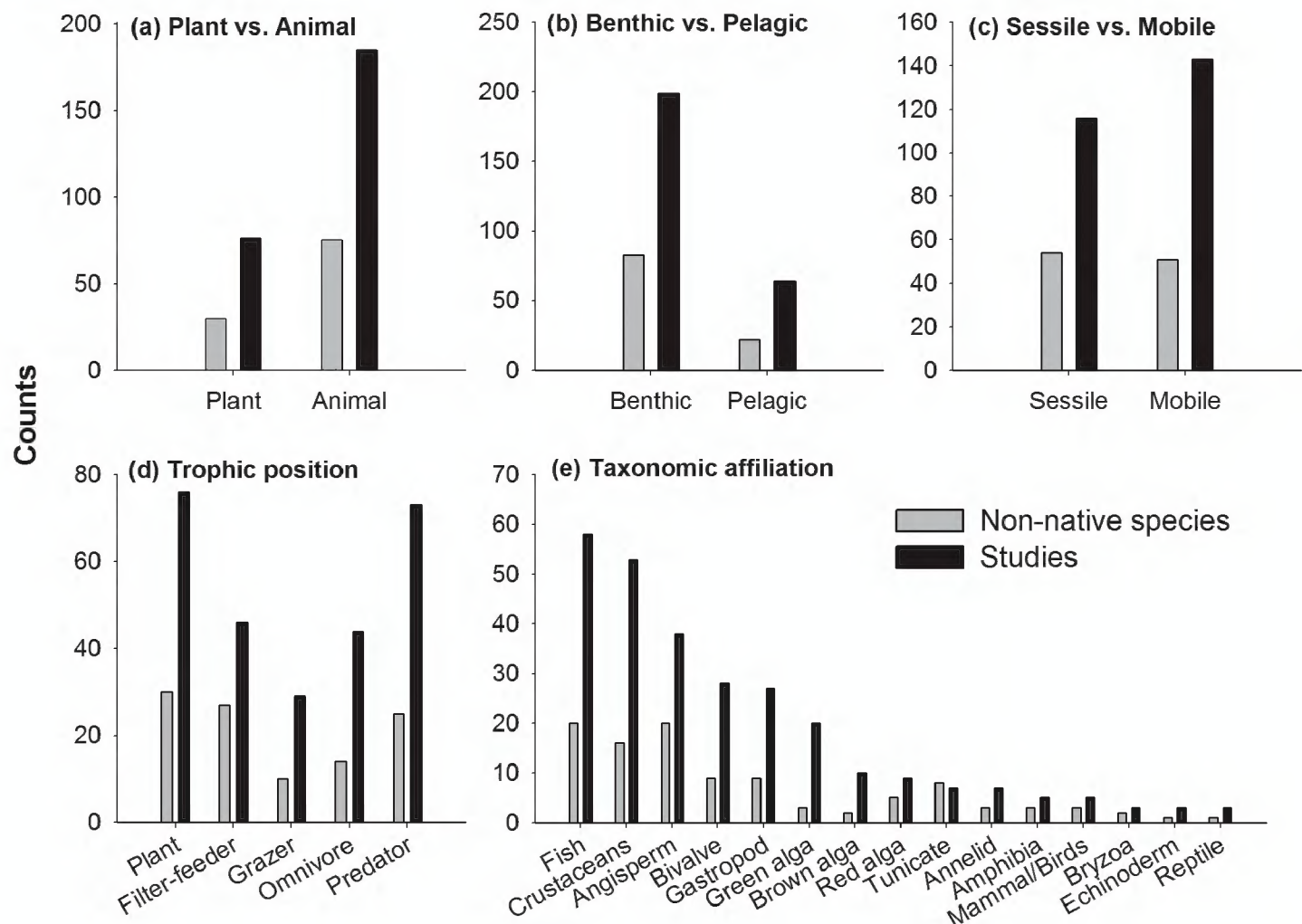
Figure 2. Aquatic invasion impact experiments classified by the attributes of the non-native species. Grey bars correspond to number of invasive species studied (total of 105 taxa); black bars correspond to the number of scientific studies (total of 259 studies). Non-native species were classified as **a** being a plant or animal **b** if they occupy the benthic or pelagic realm **c** if they are sessile or mobile **d** according to their trophic position (mud-eaters were classified as herbivores, as they consume diatoms), and **e** taxonomic affiliation.

Discussion

Virtually all the aquatic invasion examples presented in Charles Elton's seminal book "The Ecology of Invasions by Animals and Plants" were based on anecdotal or observational data (Elton 1958), yet over the past half-century, intensive field experimentation evaluating the potential impact of non-native species have emerged. Today, invasion impacts have been quantified in field experiments for >100 aquatic non-native species published in at least 259 peer-reviewed papers. From this rapidly growing literature we identified taxonomic groups, regions and habitats that have been poorly studied and where additional experimental data are needed to improve our mechanistic understanding of how non-native species impact resident species, and to guide future research and management priorities. More specifically, we highlight that to provide general impact predictions, more experiments including more non-native species are needed from open coast sandy sediments, coral reefs, polar and tropical regions, the African continent, and on herbivores, as well as marine fish, crustaceans and cnidarians. Furthermore, invasion regulations and management standards are defined and set at the level of country, yet only 10 countries have tested for impacts of

≥5 different non-native species. Addressing these research gaps will allow researchers and managers to build stronger predictive models on how non-native species impact aquatic systems across taxa, habitats and biogeographical regions.

Attributes of individual studies. We found an exponential increase in experimental impact studies over the past few decades. If this trend continues, >500 experimental aquatic impact studies could be published in the next decade. It is vital that this (expensive) effort builds on previous research rather than repeats it; i.e., new experiments should be conducted in a context of the listed studies in the Suppl. material 1. For example, c. 5% of reviewed studies were spatially pseudo-replicated, a design that should be avoided whenever possible (although in some cases this may be impossible, especially for broad-scale studies) (Hargrove and Pickering 1992; Oksanen 2001; Wernberg et al. 2012). Still, this is a low percentage compared to other past ecological research fields (Hurlbert 1984; Wernberg et al. 2012), probably reflecting that experimental invasion biology is a relatively new and modern science (Fig. 1a) and that many non-native species can be manipulated *in situ* in small plots allowing for true replication. We also found that 14% of reviewed studies did not report any measure of variability around reported average impacts; and many more studies reported incomplete data variability (Fig. 1b). Not reporting variability around mean impacts implies that the experiments cannot be included in certain meta-analyses, thereby reducing its value in synthetic frameworks (Gurevitch and Hedges 1999). Given that it is a standard protocol to replicate randomly allocated treatments and controls, it could also be considered standard to report mean impact and associated data variability (if not in a paper then in online appendix) to provide a comparative scientific baseline and to allow for future re-analysis within synthetic frameworks.

We also noted that it was common practice to pool non-significant treatments, to not report non-significant effects, or to report only a subset of quantified responses. If future studies continue to value significance over effect size, for example only reporting significant results (the extreme case being the unknown number of studies that are never published because there are no significant results), the focus will remain on "high-impact invaders" only, thereby limiting our ability to understand contextual differences between high and low invasion impact (Pyšek et al. 2008; Ricciardi and Kipp 2008; Thomsen et al. 2011). We acknowledge that publications should be concise and sacrifice information, but suggest that average values and data variability are reported for all treatments on all responses at least in online appendices. Implementing such practices will make research more transparent and simpler to evaluate, and make it possible to extract unbiased data to build strong synthetic models across studies, ecosystems and habitats (Fernandez-Duque and Valeggia 1993). Almost half of all studies reported impacts on community metrics (Fig. 1c), thereby addressing a previously highlighted research gap (Parker et al. 1999). However, only few studies reported, in the same paper, impacts on 5 community metrics (Hejda and Pyšek 2006; Albins 2013) or showed mean impacts and associated variation from all treatments on all identified taxa (Casas et al. 2004; Ross et al. 2007). Community-impact experiments with extensive data-reporting are important to facilitate a better understanding on how non-native
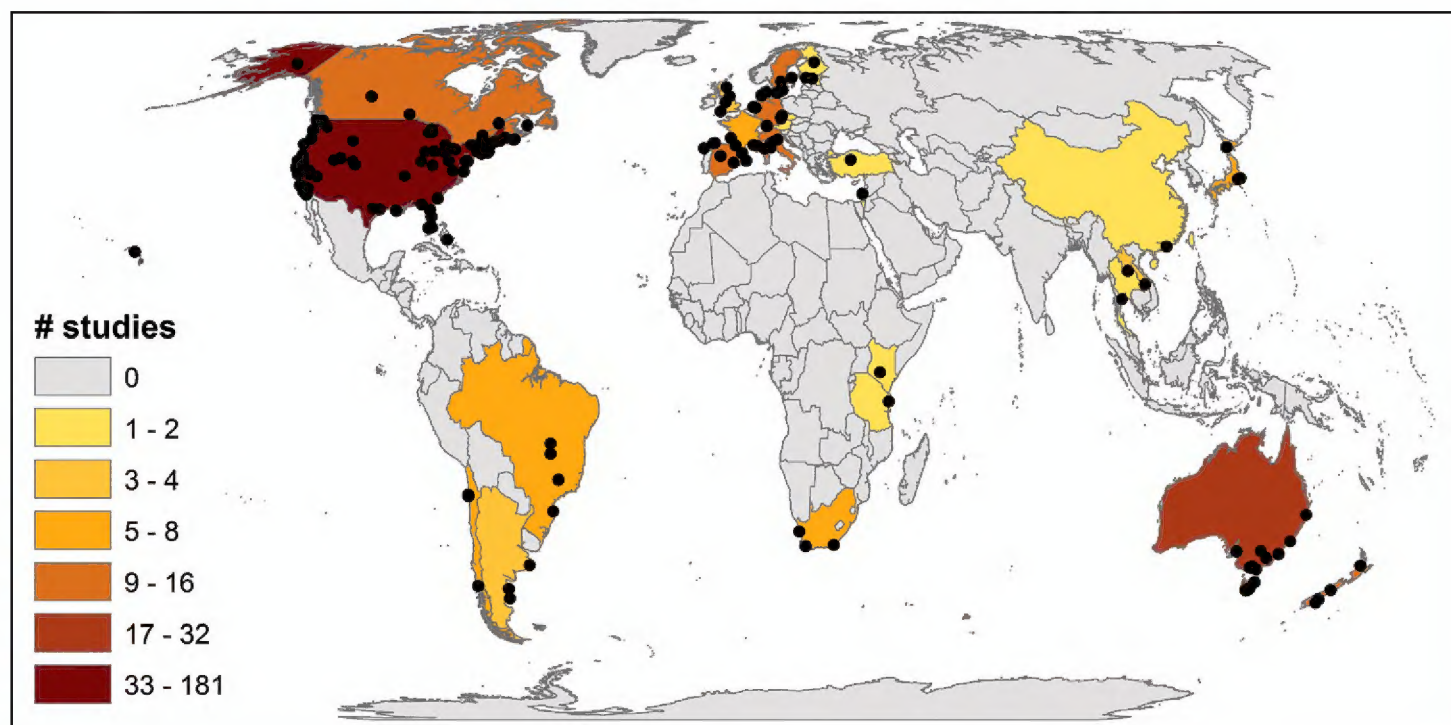
Figure 3. Global distribution of field based aquatic invasion impact experiments (*n* = 301; 259 reviewed studies + 42 extra locations from nested or multiple spatially separated experiments within studies).

species affect resident species because they, within a single environmental context, can quantify direct and indirect, strong and weak, and inter vs. intra-trophic effects.

Our literature list indicates that aquatic impact studies may have been overlooked in invasion biology. As stated in the introduction, reviews of plant invasion impacts have not included examples of impacts of seaweeds or seagrasses (cf. reviewed reference listings, Powell et al. 2011; Vilà et al. 2011; Pyšek et al. 2012), even though we reviewed 42 and 5 experimental impact studies on these two groups of marine invaders, respectively (Suppl. material 1). Similarly, an exhaustive analysis on research bias in invasion biology covering both aquatic and terrestrial systems, experimental and mensurative data, invasion impact and invasion success topics, and field and laboratory methodologies, may have underestimated aquatic invasions (Pyšek et al. 2008). For example, Pyšek et al. (2008) identified the first invasion paper from 1980 (Barrows), but we found, in our more constrained/specific review, three earlier examples (Hurlbert et al. 1972; Lubchenco 1978; Lubchenco and Menge 1978) and identified 2× and 1.3× more studies on invasions from non-native tunicates and *Carcinua maenas*, respectively. If aquatic studies continue to be under-represented in general invasion impact reviews, scientists may miss opportunities to build strong models and theories across ecosystems, and managers, conservationist and politicians who may manage linked terrestrial and aquatic systems may receive biased information about invasion impacts in their regulatory units.

Attributes of the non-native species. More than twice as many non-native animal species than plants have been tested in field impact experiments, most likely reflecting the fact that more non-native animals than plants have been found (Pyšek et al. 2008; Hewitt and Campbell 2010). However, non-native sessile organisms (plants + sessile animals) have been experimentally studied to the same degree as invasive mobile animals, despite the latter being a more species-rich group. Over-representation of

sessile species is not surprising because they are classical ecological test organisms (e.g., Connell 1961), are important in invasion biology because they are transported around the world on ship hulls (Hewitt and Campbell 2010), are relatively simple to manipulate and provide good systems to test invasion theories (Stachowicz et al. 2002; Dunstan and Johnson 2004), and can be habitat-formers and ecosystem engineers with disproportionally large effects on community structures (Crooks 2002; Ward and Ricciardi 2007; Thomsen et al. 2010). We found four times more benthic species studied than pelagic, in part reflecting that there are more of them (they include diverse marine biofouling communities) (Hewitt and Campbell 2010), in part because pelagic organisms are more difficult to control and manipulate in field experiments. It is note-worthy, however, that non-native freshwater fish, many of which are predominantly pelagic, were well-studied, which highlights that mesocosms and caging have success-fully been used to quantify impacts of these species.

Analysis across trophic levels revealed that non-native herbivores have been poorly studied. Studies are clearly needed on more aquatic herbivores to better understand, predict and manage their impacts on aquatic plant communities (Lubchenco 1978; Eastwood et al. 2007) and/or provide resource subsidies for higher trophic levels (Trussell et al. 2002). Most experiments on non-native animals were conducted with filter-feeders, for the same reasons listed above for sessile species (most sessile animals are filter-feeders). The plethora of experiments conducted with sessile filter-feeders also highlights a key difference between aquatic and terrestrial invasion ecology in that terrestrial systems have no ecologically equivalent organisms.

Only 2% of recently tallied marine non-native and cryptogenic species have been tested in field impact experiments, demonstrating that basic mechanistic insight on impact is lacking for most marine non-native species. This number varied with taxonomic groups from 0% (e.g. cnidarians, porifera) to 22% (angiosperms). We found few experimental impact studies conducted on non-native cnidarians, porifera, annelids, bryozoans, echinoderms, amphibians, mammals, or reptiles, reflecting in part, that there are few species in these groups (at least for marine organisms, Fig. 5, Hewitt and Campbell 2010). Molluscs, angiosperms and tunicates were over-represented (Fig. 5c) whereas marine fish, crustacean and cnidarians were under-represented. The former taxa are sessile or slow-mobile, easy to manipulate, and typically provide important ecosystem services by controlling ecosystem fluxes and patterns of biodiversity (Crooks 2002; Thomsen et al. 2010), whereas the latter group are more difficult to manipulate; for example, manipulating many non-native marine fish and cnidaria requires large mesocosms/cages, and many crustaceans are small and cryptic. More specifically, invasion impacts of marine fish have only been tested in two studies, both on the decorative territorial lionfish on tropical reefs, even though 166 marine fish invaders have been tallied (Hewitt and Campbell 2010). By contrast, impacts on freshwater fish have been tested on 19 out of the approximately 422 (5%) non-native species that occur globally. There are several possible reasons why there are more experimental studies on freshwater than marine invasive fish. First, based on current estimates, there appear to be more freshwater than marine non-native fish species (this needs to be
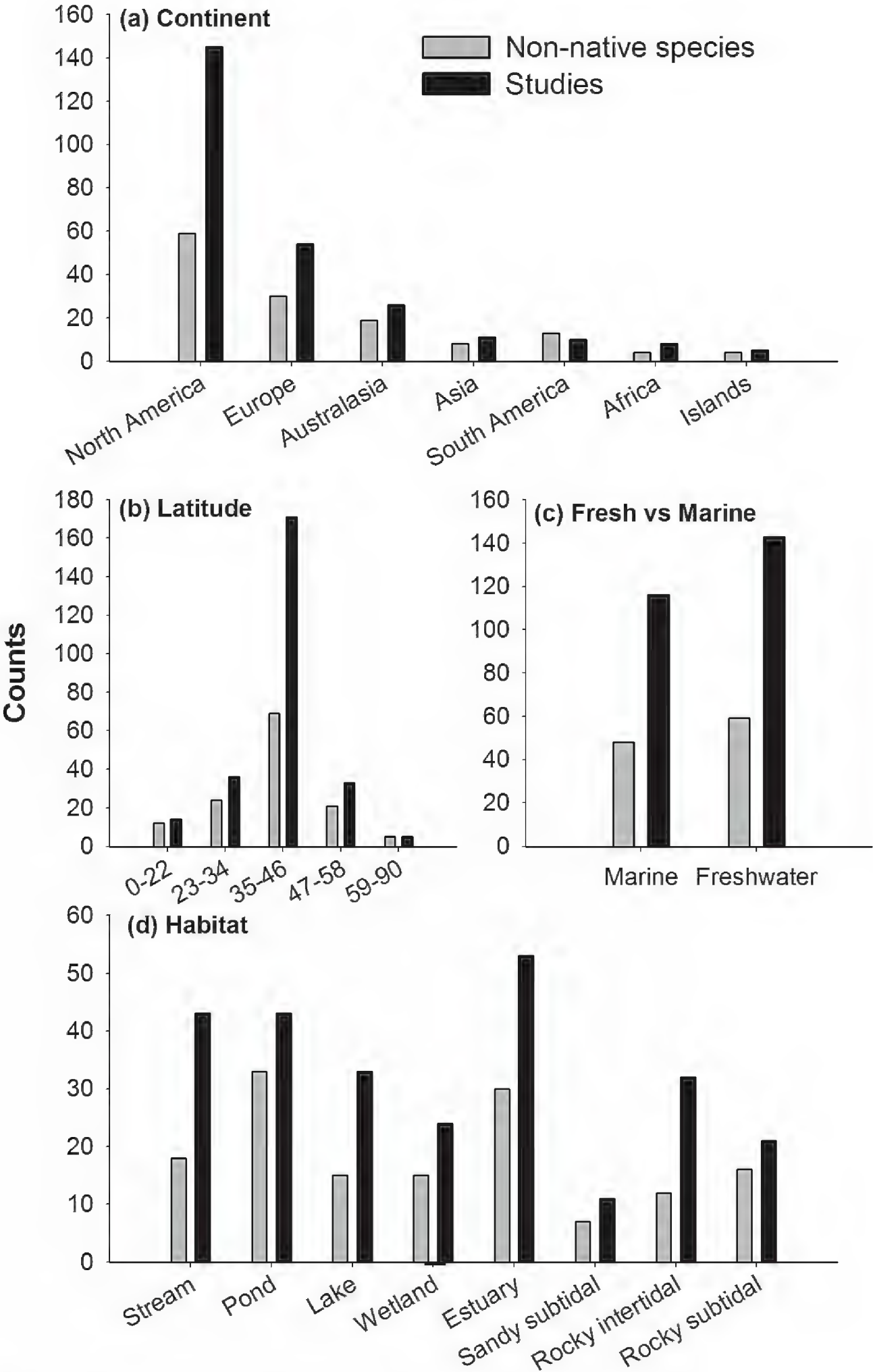
Figure 4. Aquatic invasion impact experiments classified by the attributes of the invaded system. Grey bars correspond to number of non-native species studied out of 105 taxa, and black bars correspond to the number of scientific studies out of 259. The invaded system was classified according to **a** continent **b** latitude **c** if it was a marine or freshwater system, and **d** habitat.

verified in the peer-reviewed literature). Secondly, many non-native freshwater fish are important economically, for recreational purposes, have been intentionally introduced to control diseases and weeds or to establish a fishery (Hofkin et al. 1991; Hart and Pitcher 1995; Pipalova 2006), and occur in less open and more accessible habitats than most marine species. Finally, freshwater fishes are often better adapted to survive in small-scale enclosed mesocosms (i.e. are easier to conduct experiments with) and, due to their enclosed nature, freshwater systems are amendable to whole-lake and whole-stream experiments where invasion densities are manipulated in replicated experiment at the system level (Pope et al. 2009).

Attributes of the invaded system. Not surprisingly, we found strong geographical patterns; many more aquatic invasion impact studies have been done in North America than in other countries or continents. Analysing biogeographical patterns in more detail for marine non-native species revealed a similar pattern; studies from the NE Pacific and NW Atlantic were over-represented (Fig. 4d) compared to most other marine regions. Scientific over-representation from North America, Europe and Australasia, has been documented across ecological sciences, including research on climate changes (Wernberg et al. 2012), terrestrial ecosystems (Martin et al. 2012), conservation (Clark and May 2002; Lawler et al. 2006; Darwall et al. 2011) and invasions (Pyšek et al. 2008). This geographical pattern is likely associated with historical and present-day intensive economic-related activities, such as high transport of goods and people across international borders, and therefore high propagule pressure (Pyšek et al. 2010), that many universities/researchers are located there, and that better historical and taxonomic baseline data makes it easier to identify what is native, cryptogenic and introduced. Note however, that dramatic historical invasions are still being identified also from intensively studied areas (Thomsen et al. 2006; Blakeslee and Byers 2008).

We also noted that invasion impacts have been tested with few non-native species for the majority of countries, a typical spatial unit with a specific set of management rules and regulations for invasive species. Given that invasion impacts can depend strongly on the local and regional context (Strayer et al. 2006; Thomsen et al. 2011), this low level of 'invasion impact replication', even at broad country scales, makes it difficult to build predictive impact models for most regions around the world. Latitudinal patterns mirrored patterns observed between continents, oceans and countries with 66% of all studies being conducted within a relatively narrow mid-latitudinal band. By contrast, few studies were conducted at low or high latitudes, and no studies were conducted beyond 65° - possible reflecting lacking baseline information, few researchers, and logistically challenging environments (Martin et al. 2012) and/or a real pattern of relatively fewer non-native species in polar and tropical regions (in particular for marine systems, Ruiz et al. 1999). However, for freshwater non-native species we expected more field experiments to be conducted in the tropics, because mensurative data suggest relatively large impacts in subtropical and tropical ponds and lakes from intentional fish and crustacean introductions (Miller 1989; Fernando 1991; Ogutu-Ohwayo 1993; Hart and Pitcher 1995) - the textbook case study being how the Nile perch *Lates niloticus* has contributed to
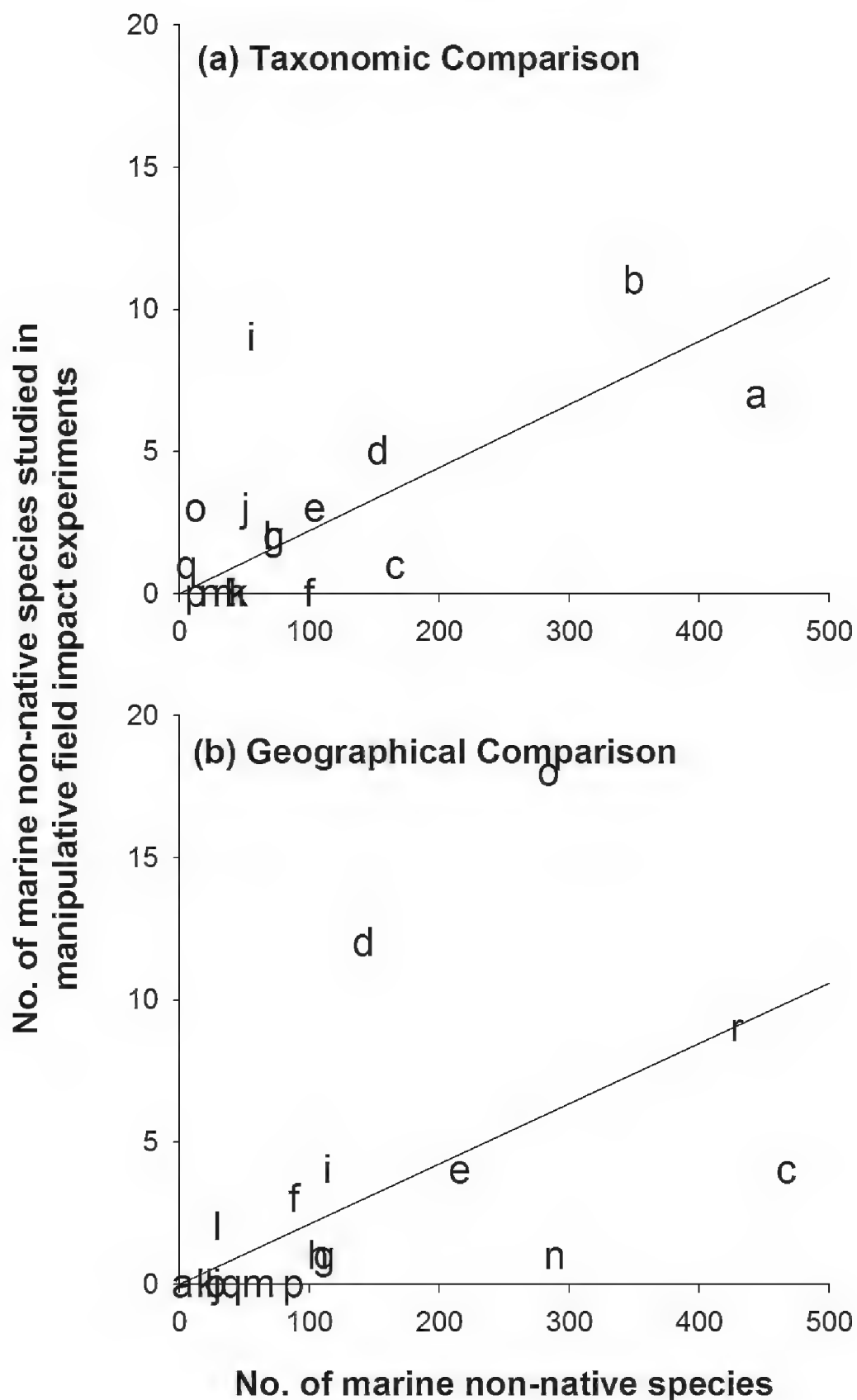
Figure 5. Marine invasion impact experiments classified according to **a** taxonomic identity of the non-native species and **b** invaded biogeographical regions. Graphs depict linear regression between *manipulative marine field-based invasion impact studies* against the total number of *non-native and cryptogenic marine species*, see manuscript text for regression data. Abbreviations (following Pyšek et al. 2008 and Hewitt and Campbell 2010); **a**: a = Arthropoda; b = Mollusca; c = Fish, d = Rhodophyta; e = Annelida; f = Cnidaria; g = Heterokontophyta; h = Ectoprocta; i = Chordata (minus fish); j = Green; k = Bacillariophyta; l = Porifera; m = Dinoflagellates; n = Platyhelminthes; o = Magnoliophyta; p = Protozoa; q = Echinodermata. **b:** a = Antarctica; b = Arctic; c = Mediterranean; d = NW Atlantic; e = NE Atlantic; f = Baltic Sea; g = Wider Caribbean; h = W Africa; i = S Atlantic Ocean; j = Central Indian Ocean; k = Arabian Sea; l = E Africa; m = E Asian Seas; n = S Pacific ocean; o = NE Pacific ocean; p = NW Pacific ocean; q = SE Pacific ocean; r = Australia & New Zealand.

extinction of endemic cichlids fishes (Ogutu-Ohwayo 1993), but supported by little experimental evidence.

Research gaps associated with invaded habitat attributes were less pronounced compared to the geographical patterns, as also noted more generally for all types of invasion studies (Pyšek et al. 2008). Thus, invaded freshwater and marine ecosystems were both represented with more than 100 studies and most aquatic habitat has been included in field based impact studies (Fig. 4d). Still, relatively few experiments have been conducted in sandy open subtidal habitats and on coral reefs. Open sandy habitats have relatively few species in low densities (Defeo et al. 2009) and probably also have few invaders (Hewitt and Campbell 2010) but coral reefs may be significantly understudied. For example, >100 marine non-native species have been registered in Hawaii alone, with many on coral reefs (Coles and Eldgredge 2002), and many species have been intentionally introduced for aquaculture, some of which have spread to adjacent reefs (Russell 1983). Alternatively, there may be few outbreaks of non-native species on coral reefs compared to more common outbreaks of native species, including diseases, seaweeds, urchins and sea stars (Lessios 1995; McCook et al. 2001; Bruno et al. 2003). Finally, we found most non-native species to be studied in freshwater ponds, largely because of common use of outdoor mesocosms in freshwater studies (Suppl. material 1), where water, plants and/or animals have been added to tanks to create semi-natural pond test systems [indeed the first identified invasion impact experiment, published in *Science* four decades ago, was a pond-mesocosm experiment (Hurlbert et al. 1972)].

Conclusions

Over the past four decades, invasion impacts have been quantified in field experiments for more than 100 aquatic non-native species published in at least 259 peer-reviewed papers. However, despite this intensive research, our ability to make generalizations and predictions remain limited because impact depends on the specific context that links attributes of the non-native species and the invaded system. Regardless of the large experimental effort, our review revealed substantial gaps in the collective knowledge. Specifically, of the 101 test species, only one was a marine fish and only six were herbivores. Similarly, of the 259 papers, only 3% were from Africa, <2% from high latitudes and only 1% from coral reefs. We therefore recommend that future experiments target these less studied non-native species, regions and habitats. We also noted that it is standard to pool or not report non-significant treatments and responses, a procedure that limits synthetic advancement by biasing meta-analysis and by making it difficult to identify invaders and environmental conditions that result in weak impacts. We therefore also recommend to report non-significant and low impact data with associated data-variability (or for continuous design show scatter-plots with explicit identification of overlapping points) and to report non-pooled impact data for all treatments and responses (even if just in online appendixes). We suggest that our

ability to extrapolate impact assessments across space, time and taxa will increase significantly if these research gaps are targeted. More generally, we argue that impact experiments should manipulate new and novel combinations of different non-native species, different invaded places, different resident organisms, different abiotic conditions and different resource levels, than has already been tested in past experiments (cf. Suppl. material 1). In conclusion, the last 40 years of research activity has provided an excellent starting point to understand invasion impact mechanistically, but we are still far from being able to build generalized and predictive models of invasion impacts on local management scales of most invaders.

Acknowledgements

References

Airoldi L (2000) Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. Ecology 81: 798–814. doi: 10.1890/0012-9658(2000)081[0798:EODLHA]2.0.CO;2

Albins M (2013) Effects of invasive Pacific red lionfish, *Pterois volitans*, versus a native predator on Bahamian coral-reef fish communities. Biological Invasions: 1–15. doi: 10.1007/s10530-012-0266-1

Barrows EM (1980) Robbing of exotic plants by introduced Carpenter and Honey Bees in Hawaii, with comparative notes. Biotropica 12: 23–29. doi: 10.2307/2387770

Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80: 2711–2726. doi: 10.1890/0012-9658(1999)080[2711:TTRCOP]2.0.CO;2

Blakeslee AMH, Byers J (2008) Using parasites to inform ecological history: comparisons among three congeneric marine snails. Ecology 89: 1068–1078. doi: 10.1890/07-0832.1

Bruno JF, Fridley JD, Bromberg K, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Gaines SD, Stachowicz JJ (Eds) Species Invasions: Insights into Ecology, Evolution and Biogeography Sinauer, Sunderland, MA, 13–40.

Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. Ecology Letters 6: 1056–1061. doi: 10.1046/j.1461-0248.2003.00544.x

Byers J, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson AE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impact of nonindigenous species. Conservation Biology 16: 630–640. doi: 10.1046/j.1523-1739.2002.01057.x

Byers JE (2009) Competition in marine invasions. In: Rilov G, Crooks JA (Eds) Biological Invasions in Marine Ecosystems – Ecological, Management, and Geographic Perspectives. Springer-Verlag, Herdelberg, 245–260.

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78: 97–106. doi: 10.1016/0006-3207(96)00020-1

Casas G, Scrosati R, Piriz ML (2004) The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions 6: 411–416. doi: 10.1023/B:BINV.0000041555.29305.41

Clark JA, May RM (2002) Taxonomic Bias in Conservation Research. Science 297: 191–192. doi: 10.1126/science.297.5579.191b

Coles SL, Eldgredge LG (2002) Nonindigenous Species Introductions on Coral Reefs: A Need for Information. Pacific Science 56: 191–209. doi: 10.1353/psc.2002.0010

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecological Monographs 42: 710–723.

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153–166. doi: 10.1034/j.1600-0706.2002.970201.x

Cucherouset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. Fisheries 36: 215–230. doi: 10.1080/03632415.2011.574578

Darwall WRT, Holland RA, Smith KG, Allen D, Brooks EGE, Katarya V, Pollock CM, Shi Y, Clausnitzer V, Cumberlidge N, Cuttelod A, Dijkstra K-DB, Diop MD, García N, Seddon MB, Skelton PH, Snoeks J, Tweddle D, Vié J-C (2011) Implications of bias in conservation research and investment for freshwater species. Conservation Letters 4: 474–482. doi: 10.1111/j.1755-263X.2011.00202.x

Defeo O, McLachlan A, Schoeman DS, Schlacher TA, Dugan J, Jones A, Lastra M, Scapini F (2009) Threats to sandy beach ecosystems: a review. Estuarine, Coastal and Shelf Science 81: 1–12. doi: 10.1016/j.ecss.2008.09.022

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? Trends in Ecology and Evolution 20: 470–474. doi: 10.1016/j.tree.2005.07.006

Dunstan PK, Johnson CR (2004) Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. Oecologia 138: 285–292. doi: 10.1007/s00442-003-1400-7

Eastwood MM, Donahue MJ, Fowler AE (2007) Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors. Biological Invasions 9: 397–407. doi: 10.1007/s10530-006-9041-5

Elton CS (1958) The ecology of invasions by animals and plants. Mathuess, London, 1996.

Fernandez-Duque E, Valeggia C (1993) Meta-analysis: a valuable tool in conservation research. Conservation Biology 8: 555–561. doi: 10.1046/j.1523-1739.1994.08020555.x

Fernando CH (1991) Impacts of Fish Introductions in Tropical Asia and America. Canadian Journal of Fisheries and Aquatic Sciences 48: 24–32. doi: 10.1139/f91-301

Forrest BM, Taylor MD (2003) Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. Biological Invasions 4: 375–386. doi: 10.1023/A:1023613428351

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends in Ecology & Evolution 17: 22–27. doi: 10.1016/S0169-5347(01)02358-8

Grosholz ED, Ruiz G (2009) Multitrophic effects of invasion in marine and estuarine systems. In: Rilov G, Crooks JA (Eds) Biological Invasions in Marine Ecosystems – Ecological, Management, and Geographic Perspectives. Springer-Verlag, Herdelberg, 305–324.

Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. Ecology 80: 1142–1149. doi: 10.1890/0012-9658(1999)080[1142:SIIEMA]2.0.CO;2

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19: 470–474. doi: 10.1016/j.tree.2004.07.005

Hargrove WW, Pickering J (1992) Pseudoreplication: a sine qua non for regional ecology. Landscape Ecology 6: 251–258. doi: 10.1007/BF00129703

Hart P, Pitcher TJE (1995) The Impact of Species Changes in African Lakes. Fish & Fisheries Series 18: 640.

Hejda M, Pyšek P (2006) What is the impact of *impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation 132: 143–152. doi: 10.1016/j.biocon.2006.03.025

Hewitt CL, Campbell ML (2010) The relative contribution of vectors to the introduction and translocation of marine invasive species. Australian Department of Agriculture Fisheries, and Forestry, Canberra, 56.

Hoeffle H, Thomsen MS, Holmer M (2011) High mortality of *Zostera marina* under high temperature regimes but minor effects of the invasive macroalgae *Gracilaria vermiculophylla*. Estuarine, Coastal and Shelf Science 92: 35–46. doi: 10.1016/j.ecss.2010.12.017

Hofkin BV, Mkoji GM, Koech DK, Loker ES (1991) Control of schistosome-transmitting snails in Kenya by the North American crayfish *Procambarus clarkii*. American Society of Tropical Medicine and Hygiene 45: 339–344.

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187–211. doi: 10.2307/1942661

Hurlbert SH, Zedler J, Fairbanks D (1972) Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science 175: 639–641. doi: 10.1126/science.175.4022.639

Kimbro DL, Cheng BS, Grosholz ED (2013) Biotic resistance in marine environments. Ecology Letters 16: 821–833. doi: 10.1111/ele.12106

Kuussaari M, Bommarco R, K. R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà R, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution 24: 564–571. doi: 10.1016/j.tree.2009.04.011

Lawler JJ, Aukema JE, Grant JB, Halpern BS, Kareiva P, Nelson CR, Ohleth K, Olden JD, Schlaepfer MA, Silliman BR, Zaradic P (2006) Conservation science: a 20-year report card. Frontiers in Ecology and Environment 4: 473–480. doi: 10.1890/1540-9295(2006)4[473:CSAYRC]2.0.CO;2

Lessios HA (1995) *Diadema Antillarum* 10 years after mass mortality - still rare, despite help from a competitor. Proceedings of the Royal Society of London - Series B: Biological Sciences 259: 331–337. doi: 10.1098/rspb.1995.0049

Lockwood JL, Hoopes MF, Marchetti P (2007) Invasion ecology. Blackwell Publishing.

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist 112: 23–39. doi: 10.2307/2937360

Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. Ecological Monographs 59: 67–94.

Martin LJ, Blossey B, Ellis E (2012) Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Frontiers in Ecology and the Environment 10: 195–201. doi: 10.1890/110154

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19: 400–417. doi: 10.1007/s003380000129

Miller DJ (1989) Introductions and extinction of fish in the African great lakes. Trends in Ecology and Evolution 4: 56–59. doi: 10.1016/0169-5347(89)90145-6

Ogutu-Ohwayo R (1993) The effects of predation by Nile Perch, *Lates niloticus* L., on the fish of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 7: 701–711. doi: 10.1046/j.1523-1739.1993.07030701.x

Oksanen L (2001) Logic or experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94: 27–34. doi: 10.1034/j.1600-0706.2001.11311.x

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19: 18–23. doi: 10.1016/j.tree.2003.09.010

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham MJ, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JL, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19. doi: 10.1023/A:1010034312781

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2000) Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment 84: 1–20. doi: 10.1016/S0167-8809(00)00178-X

Pipalova I (2006) A review of grass carp us for aquatic weed control and its impact on water bodies. J Aquat Plant Manage 44: 1–12.

Pope KL, Piovia-Scott J, Lawler SP (2009) Changes in aquatic insect emergence in response to whole-lake experimental manipulations of introduced trout. Freshwater Biology 54: 982–993. doi: 10.1111/j.1365-2427.2008.02145.x

Powell KI, Chase JM, Knight TM (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. Am J Bot 98: 539–548. doi: 10.3732/ajb.1000402

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18: 1725–1737. doi: 10.1111/j.1365-2486.2011.02636.x

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau A-M, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Solarz W, Vila

M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions. Proceedings of the National Academy of Sciences 107: 12157–12162. doi: 10.1073/pnas.1002314107

Pyšek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23: 237–244.

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, 537.

Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12: 425–433. doi: 10.1111/j.1366-9516.2006.00262.x

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781–784.

Ricciardi A, Kipp R (2008) Predicting the number of ecologically harmful exotic species in an aquatic system. Diversity and Distributions 14: 374–380.

Ross DJ, Keough MJ, Longmore AR, Knott NA (2007) Impacts of two introduced suspension feeders in Port Phillip Bay, Australia. Marine Ecology Progress Series 340: 41–53.

Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography 44: 950–972.

Ruiz GM, Fofonoff PW, Steves B, Foss SF, Shiba SN (2011) Marine invasion history and vector analysis of California: a hotspot for western North America. Diversity and Distributions 17: 362–373. doi: 10.1111/j.1472-4642.2011.00742.x

Russell DJ (1983) Ecology of the red imported seaweed *Eucheuma striatum* on Coconut Island, Oahu, Hawaii. Pacific Science 37: 87–107.

Sax DF, Gaines SD (2008) Species diversity and extinction: the future of native biodiversity on islands. PNAS 105: 11490–11497. doi: 10.1073/pnas.0802290105

Simberloff D (2011) Non-natives: 141 scientists object. Nature 475: 36–36. doi: 10.1038/475036a

Sorte CJB, Ibáñez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16: 261–270. doi: 10.1111/ele.12017

Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. PNAS (USA) 99: 15497–15500. doi: 10.1073/pnas.242437499

Staehr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Marine Ecology Progress Series 207: 79–88. doi: 10.3354/meps207079

Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174. doi: 10.1111/j.1365-2427.2009.02380.x

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21: 645–651. doi: 10.1016/j.tree.2006.07.007

Sutherland WJ, Pullin AS, Dolman PM, Knight TM (2004) The need for evidence-based conservation. Trends in Ecology & Evolution 19: 305–308. doi: 10.1016/j.tree.2004.03.018

Thomsen MS, Gurgel CFD, Fredericq S, McGlathery KJ (2006) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in Hog Island Bay, Virginia: A cryptic alien and invasive macroalga and taxonomic correction. Journal of Phycology 42: 139–141. doi: 10.1111/j.1529-8817.2005.00160.x

Thomsen MS, McGlathery K (2006) Effects of accumulations of sediments and drift algae on recruitment of sessile organisms associated with oyster reefs. Journal of Experimental Marine Biology and Ecology 328: 22–34. doi: 10.1016/j.jembe.2005.06.016

Thomsen MS, Olden JD, Wernberg T, Griffin JN, Silliman BR (2011) A broad framework to organize and compare ecological invasion impacts. Environmental Research 111: 899–908. doi: 10.1016/j.envres.2011.05.024

Thomsen MS, Wernberg T, Altieri AH, Tuya F, Gulbransen D, McGlathery KJ, Holmer M, Silliman BR (2010) Habitat Cascades: The Conceptual Context and Global Relevance of Facilitation Cascades via Habitat Formation and Modification. Integrative and Comparative Biology 50: 158–175. doi: 10.1093/icb/icq042

Thomsen MS, Wernberg T, Tuya F, Silliman BR (2009) Evidence for impacts of non-indigenous macroalgae: a meta-analysis of experimental field studies. Journal of Phycology 45: 812–819. doi: 10.1111/j.1529-8817.2009.00709.x

Trussell G, Ewanchuck P, Bertness MD (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5: 241–245. doi: 10.1046/j.1461-0248.2002.00304.x

Twardochleb LA, Olden JD, Larson ER (2013) A global meta-analysis of the ecological impacts of non-native crayfish. Freshwater Science 32: 1367–1382. doi: 10.1899/12-203.1

Underwood AJ (1996) Detection, interpretation, prediction and management of environmental disturbances: Some roles for experimental marine ecology. Journal of Experimental Marine Biology & Ecology 200: 1–27. doi: 10.1016/S0022-0981(96)02637-8

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702–708. doi: 10.1111/j.1461-0248.2011.01628.x

Ward JM, Ricciardi A (2007) Impacts of *Dreissena invasions* on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13: 155–165. doi: 10.1111/j.1472-4642.2007.00336.x

Wernberg T, Smale DA, Thomsen MS (2012) A decade of climate change experiments on marine organisms: procedures, patterns and problems. Global Change Biology 18: 1491–1498. doi: 10.1111/j.1365-2486.2012.02656.x

Wilcove DS, Rothstein D, Dubow A, Phillips E, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48: 607–615. doi: 10.2307/1313420

Williams SL, Smith JE (2007) A global review of the distribution, taxonomy, and Impacts of Introduced Seaweeds. Annual Review of Ecology, Evolution, and Systematics 38: 327–359. doi: 10.1146/annurev.ecolsys.38.091206.095543

Supplementary material I

List of reviewed references.

Authors: Mads S. Thomsen, Thomas Wernberg, Julian D. Olden, James E. Byers, John F. Bruno, Brian R. Silliman & David R. Schiel

Data type: reference list

Explanation note: References are divided into general (G), freshwater (F), aquatic (FM) or marine (M) journals. References with an asterisk (*) did not replicate or pseudo-replicated either treatment and/or control plots.

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